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IS THERE A DOWNWARD TRANSPORT OF ORGANIC MATTER RELATED TO A DIEL VERTICAL MIGRATIONS OF ANIMALS IN THE OCEAN?

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ABSTRACT. The downward transport of organic matter by means of diel vertical migrations of planktonic animals consists of (1) flux of organic material forming the bodies of migrating animals, and (2) active transport of gut contents of the migrants. In the first case the magnitude of transport is determined by the biomass of migrating animals consumed by predators in the deep layer and the amount of food ingested by migrators at the same depth. It is shown that even under conditions of low feeding rate in the deep layer, downward transport of organic matter in this manner is negligible. The transport of organic matter in gut contents is possible only with macropanktonic animals but even in this case it comprises a very small fraction of the total downward flux of organic matter in oceanic system.

Key words: downward transport, organic matter, vertical migrations, ocean ecosystem

Although the idea that vertical migration of pelagic animals in the ocean may be the means of transport of organic matter into the deep layers has a long history (Vinogradov 1953, 1955, 1968, Tchindonova 1959, Banse 1964, Tseitlin 1982), the quantitative data confirming this hypothesis were absent. Using the data on the migrations of major groups of plankton from the Canary Island region an attempt is made here to evaluate the transport of organic matter in the diel vertical migrations of pelagic animals.

Average daily transport of organic matter in vertical migrations of animals

Usually migrating animals rise to the upper water layer which is richer in food, feed there, and then descend serving themselves as food for animals living in deep layer. Thus the transportable organic matter is the material of migrating animals. This is here called a transport of living organic matter (the other possibility is vertical transport of dead organic matter in the form of gut contents of migrators, which we will discuss below).

Obviously, in a stationary condition the maximum quantity of organic matter which can be transported downward during the day by a group of migrating animals is equal to the daily production P_m of this group. This maximum transport value occurs when the migrators feed only at the upper depth and are consumed themselves only at the lower depth. In this case migrators fulfill the transport function in ideal fashion. More realistic is the situation in which the migrators feed and are themselves eaten at both the upper and lower depths. Let us find the formula which gives the amount of transport for this case. To simplify the problem, we will consider that the migrators spend half of their time at the upper depth (z_u) and half at the lower depth (z_l). At any time migrators occupy more or less extended layers; z_u and z_l are the mean depths of such layers at night and day respectively. Then the total elimination E of the migrating animals can be expressed in the form:

$$E = E(z_l) + E(z_u), \qquad (1)$$

where $E(z_l)$ is the elimination in the deep waters z_l, and $E(z_u)$ is the elimination at the upper level, z_u. We ignore the mortality unrelated to predation and assume that all eliminated migrators were eaten by predators. We can then write the following equation:

$$E(z_u)/E(z_l) = C(z_u)/C(z_l), \qquad (2)$$

where $C(z)$ is the consumption of migrators by predators at the depth z. Since in stationary conditions production P_m is equal to elimination E, it follows from the equation (1) that

$$P_m = E(z_l) + E(z_u). \qquad (3)$$

From equations (2) and (3) we find

$$E(z_l) = P_m / \left[1 + \frac{C(z_u)}{C(z_l)}\right]. \quad (4)$$

The consumption at the depth z can be presented in the form (Tseitlin 1981 b):

$$C(z) = B(z)\, f(W)/\tau(z)\, T_0(z), \quad (5)$$

where $B(z)$ is the biomass of mesoplankton at the depth z, $\tau(z)$ is the temperature correction for respiration at this depth; $T_0(z)$ is a parameter in the equation determining the duration of growth in the animals $T(z) = T_0(z)\, W^{0.25}\tau(z)$; and $f(W)$ is a function of the body mass W of animals independent of z. As shown by Tseitlin (1983),

$$T_0(z) = T_{0s} B_s \tau_s / B(z)\, \tau(z), \quad (6)$$

where T_{0s} is a constant, and B_s, and τ_s, the values of B and τ in the surface layer. Substituting equation (6) into the equation (5), we obtain

$$C(z) = B^2(z) f(W)/T_{0s} B_s \tau_s. \quad (7)$$

From equations (7) and (4) we have:

$$E(z_l) = P_m / \left[1 + \frac{B^2(z_u)}{B^2(z_l)}\right] \quad (8)$$

In particular case of migration in tropic regions of the ocean in the 100-1000 m layer, we may use the following formula for $B(z)$ (Tseitlin 1981 b): $B(z) = 100\, B_s/z$, where z in meters. Substituting this into equation (8), we obtain:

$$E(z_l) = P_m / [1 + (z_l/z_u)^2] \quad (9)$$

This equation determines the elimination of migrants per day at depth z_l.

The transport of living organic matter takes place only when $E(z_l)$ i. e., the quantity of organic material given up to the predators at depth z_l, is greater than that which the migrants obtain by feeding at this depth (and the feeding does not occur in the deeper layer (Donaldson 1975, Kinzer 1977)). Otherwise there is only the transport of organic matter along the food chain at depth z_l. If we designate the food consumption by migrants at z_l as $C_m(z_l)$, and the transport as $\varepsilon(z_l)$, we can write:

$$\varepsilon(z_l) = \begin{cases} E(z_l) - C_m(z_l) & \text{when } E(z_l) > C_m(z_l) \\ 0 & \text{when } E(z_l) \le C_m(z_l) \end{cases} \quad (10)$$

Since the transport of organic matter to depth z_l is the transmission of organic matter obtained through feeding at the upper depth to the next trophic level at depth z_l, negative values of ε in the equation (10) would indicate that organic matter was transmitted to the next trophic level through feeding at the lower depth, and thus that there was no transport of organic matter.

Let us determine the magnitude of the food intake at the lower depth $C_m(z_l)$ at which there is no transport of organic matter by the migrators. The production of migrators P_m is related to their total food intake C_{ms} (the sum of the ingestion at z_u and z_l) by the equation $P_m = UK_2C_{ms}$, where U is the assimilation efficency, $K_2 \equiv P_m/(P_m + R_m)$ is the efficiency of utilization of assimilated food for growth, and R_m is the loss of energy through respiration. Substituting this expression for P_m into equation (9) and the resulting equation into equation (10), gives:

$$\varepsilon(z_l) = UK_2C_{ms}[1 + (z_l/z_u)^2] - C_m(z_l). \quad (11)$$

From the condition that there is no transport of organic matter, $\varepsilon(z_l) = 0$, we find:

$$\frac{C_m(z_l)}{C_{ms}} = \frac{UK_2}{1 + (z_l/z_u)^2} \quad (12)$$

As we shall see below, $z_l/z_u \approx 1.7$, and accordingly $C_m(z_l)/C_{ms} \approx 0.25\, UK_2$. Assuming that $U = 0.8$ and $K_2 = 0.3$, we obtain: $C_m(z_l)/C_{ms} = 0.06$. This means that if the organisms consume less than 6% of the total diel food intake in the deep layer, there is no transport of living organic matter. But the values of U and K_2 assumed in the example are far from the lowest possible ($K_2 = 0.25$ (Humphreys 1979) and $U_2 = 0.6$ (Sushchenya 1975) we may consider as average values), and the level of consumption at depth z_l corresponding to the absence of transport may be even smaller.

The procedures which led to equation (9) allows to write an equation for $C_m(z_l)$. Using equation (5) (which we used above to calculate the consumption of migrators by predators) to evaluate the food consumption by migrators, we can find the ratio $C_m(z_l)/C_m(z_u)$. Since in this case T_0 is a constant, and since we can use the

approximate equation $\tau(z) = 0.043z^{0.64}$ (where z is in meters) at depths 100-1000 m for the function $\tau(z)$ presented in (Tseitlin 1982), we obtain

$$C_m(z_l)/C_m(z_u) = \gamma(z_u/z_l)^{1.64}. \quad (13)$$

We have included in the equation (13) the factor $0 < \gamma < 1$, characterizing the behavior of migrating animals. A possible (and very probable) cause of the descent of migrating animals is a weakening of their motor activity (Rudjakov 1970). Although this is not necessarily associated with decrease in feeding activity, observation on the diurnal behavior of Mictophidae from the bathyscaphe (Barham 1971) indicates that this does hold true for them at least. A weakening of feeding activity at the lower depth is characterized by the multiplier γ in equation (13). From equation (13) and the equation $C_{ms} = P_m/UK_2 = C_m(z_l) + C(z_u)$ we obtain

$$C_m(z_l) = \frac{P_m}{UK_2[1 + \frac{1}{\gamma}(z_l/z_u)^{1.64}]} \quad (14)$$

Substituting equations (9) and (14) into the equation (10) gives:

$$\varepsilon(z_l) = \frac{P_m}{1 + (z_l/z_u)^2} - \frac{P}{UK_2[1 + \frac{1}{\gamma}(z_l/z_u)^{1.64}]} \quad (15)$$

Using the same values of U, K_2 and z_l/z_u, as in the example considered above, we see that there is no downward transport of organic matter when $\gamma \geq 0.16$.

The lack of data on the feeding of migrators at various depths does not allow to calculate precisely the transport of organic matter from equation (15). All that now can be done is to determine the maximum transport of organic matter (assuming that the migrators are eaten in the entire range of depths which they inhabit) from equation (9), ignoring the feeding at the lower depth, i.e., with $C_m(z_l) = 0$. But first we rewrite equation (9) in a slightly different form. The production P of a size group of organisms with weights between $w_{\min}$ and $w_{\max}$ can be presented in the following form (Tseitlin 1986, 1991):

$$P(z) = \frac{B_s(\bar{W}_{\min}^{-0.25} - W_{\max}^{-0.25})}{3T_0\tau_s} \cdot \left(\frac{100}{z}\right)^2 \quad (16)$$

where $W_{\min} = w_{\min}/w_0$, $W_{\max} = w_{\max}/w_0$, $w_0 = 1$ mg. Assuming that the proportion of migrants in any size subgroup of the group is constant, we may write

$$P_m = k_m P \quad (17)$$

where $k_m = N_m/N$ is the ratio of the number of migrants in the group N_m to the total number N of organisms. From equations (9) and (17) we find:

$$E(z) = k_m P/[1 + (z_l/z_m)^2] \quad (18)$$

Determination of k_m and z_l/z_u and the maximum transport from observational data

Our determination will be based on data from the SOND expedition in the vicinity of Canary Islands which were used previously to study the characteristics of vertical migration of various groups of pelagic animals (Rudjakov and Tseitlin 1976, Rudjakov 1979). In contrast to these works, we combine the organisms into two large groups to discuss their migration characteristics. In the first group we include copepods, ostracodes and amphipods, which for the most part are organisms measuring 1-10 mm. For brevity we will call this group the "mesoplankton", although it is in fact somewhat narrower. In the second group ("macroplankton") we will include euphausids, decapods and fish, i.e. organisms measuring 10-60 mm. When we mentioned the relative numbers of migrators above, we supposed that we had a method of distinguishing them from nonmigrating organisms. In reality this is not the case. The existence of diel migrations is usually confirmed by the differences between the average depth of the day and night vertical distributions of the organisms (modes or medians may be used instead of means). For many reasons, the average depths of these distributions usually differ and, therefore formally all of the animal organisms migrate. The true situation might be made clearer by long-term observations, but such data are lacking. Rudjakov (1979) distinguished migrating species by a formal criterion; he considered the species as migrating if the difference between the daytime and nighttime average depths was significant at a certain confidence level. But a small displacement at a considerable depth (e.g., 30 m at a depth of 600 m) might be significant and therefore such an approach cannot be appropriate for discussing the transport of organic matter. The significance of a rise of, say, 100 m may differ greatly depending on whether it is from depth of 200 or 800 m. In the former case, it is a displacement within an area of high temperature and food

Table 1. Calculation of maximum vertical transfer of organic matter in diel vertical migrations

Lower depth of inhabited zone z_l, m	Proportion of migrators, k_m	z_l/z_u	Δz, m	$\frac{k_m}{1+(z_l/z_u)^2}$
		Mesoplankton		
100-300	0.52	2.6	120	0.07
300-500	0.89	1.7	160	0.23
500-700	0.35	1.8	270	0.08
700-900	0.04	1.5	280	0.01
		Macroplankton		
100-300	0.06	2.2	110	0.01
300-500	0.36	2.6	250	0.05
500-700	0.42	2.9	390	0.04
700-900	0.61	2.1	430	0.11

concentration gradients, while in the latter, it takes place in an area of small gradients. Discussing the transport of organic matter we use a rather arbitrary definition of migrators. In this case we designate as migrators the animals for which the ratio between the upper and lower depths meets the condition

$$z_l/z_u \geq 1.25 \qquad (19)$$

This is equivalent to the condition $\Delta z_l/z_u \geq 0.2$, where the range of migration is $\Delta z = z_l - z_u$. In other words, we will not consider as migrators the organisms which rise by a distance equal to less then 20 % of the lower depth of inhabited zone. We then include in group of migrators organisms which perform the reverse migration (rising in the day and descending in the night), since it is unimportant at what time of day the transport of organic matter takes place if we bear in mind that the organisms feed at a depth z_u.

The table shows values of k_m and z_l/z_u (z_l/z_u is a weighted average by abundance) calculated for organisms divided into four groups in terms of the lower depth z_l which they inhabit. (The nature of the raw data does not allow us to take account of the 0-100 m layer). The migrators identified from these data by Rudjakov (1979), have very similar values of k_m and z_l/z_u in the case of mesoplankton, while the divergence is greater for the macroplankton. The reason is that in each case the macroplankton is represented by a relatively small number of species, and if one of them makes small displacements (but significant by the criteria used by Rudjakov), and if its numbers are sufficiently great, this may significantly change the calculated parameters. The estimate $z_l/z_u \approx 1.7$, which we used above, is assumed to be characteristic for mesoplankton in the layer where the potential transport magnitude is the greatest. The table shows the characteristic extents of migration Δz found from the average values of z_l/z_u. It is apparent that the magnitude of Δz is associated with the criterion which we chose (equation (19)). The quantity $k_m/[1+(z_l/z_u)^2]$ indicates the proportion of production which is transported downward with migrators. We recall that this figures give a maximum value for transport which, according to equation (1), might be decreased to zero with even a small amount of feeding of migrator at depth z_l.

Let us compare the maximum of organic matter flux produced by migrators with the downward flux of detritus at the same depth (the latter flux is unrelated to the active transport of gut content of the migrators). These fluxes should be evaluated for the depth $z_l = 300$ m since the most part of migrating animals descends down to this depth and at this depth the ratio $k_m/[1+(z_l/z_u)]$ has a maximum value 0.23 (Table 1). Let us consider that all migrators occuring in the upper 100 m layer at night, descend at z_l. (There is no doubt that such assumption overestimates the real migration). Then for the organic carbon flux F_m produced by migrators we can write the following expression:

$$F_m = \frac{100 k_m q_m P}{1+(z_l/z_u)^2}, \quad \text{mg C m}^{-2}\text{day}^{-1} \qquad (20)$$

where $q_m = 0.07$ is the organic carbon content of the bodies of migrators. For the production P one can use the equation (20) with $w_{min} = 0.04$ mg and $w_{max} = 24$ mg, that approximately corresponds to body length of 1 to 10 mm, respectively. Then it can be found:

$$F_m = 0.03\, B_s/\tau_s, \quad \text{mg C m}^{-2}\text{day}^{-1}. \quad (21)$$

As it have been shown (Tseitlin 1991), the organic carbon flux related to the sinking detritus may be estimated as:

$$F_d(z) = \frac{100 q_d (1 - K_2) P_h}{K_2} \frac{100}{z}, \quad \text{mg C m}^{-2}\text{day}^{-1},$$

where $q_d = 0.045$ is the organic carbon content of detritus, $P_h = 0.085\, B_s/\tau_s$ and $K_2 = 0.25$. With these values of parameters and $z = 300$ m:

$$F_d(300) = 0.38\, B_s/\tau_s . \quad (22)$$

From equations (21) and (22) it follows that $F_m/F_d = 0.08$, i.e. overestimated organic carbon flux produced by migrators makes up only a small fraction of that of detritus.

The comparison of F_m and F_d is of a somewhat formal nature, since fates of these fluxes are different. The major part of detritus is consumed by small organisms while migrating animals are a food source for relatively large predators. Let us estimate the food requirements of the latter.

Consumption of a size group of animals at the layer 300-500 m may be evaluated by means of the equation (Tseitlin 1981b, 1986):

$$C = \frac{1 - \eta}{UK_2} \int_{300}^{500} P(z)dz \quad (23)$$

where η = 0.1 is the coefficient of ecological efficiency (the ratio between productions of two successive trophic levels), and P is determined by the equation (16). As a rule, the body mass of predators consuming migrating animals must be 10^3-10^4 times more than that of their preys (Tseitlin 1981 a). So we have to multiply the migrator body mass by 1000 and use in equation (23) $w_{min} = 40$ mg and $w_{max} = 24$ g. Use of these values in equations (16) and (23) with $U = 0.6$ and $K_2 = 0.25$ gives:

$$C = 0.26\, B_s/\tau_s, \quad \text{mg C m}^{-2}\text{day}^{-1}$$

or

$$C = 0.018\, B_s/\tau_s, \quad \text{mg C m}^{-2}\text{day}^{-1} \quad (24)$$

It follows from equations (21) and (24) that $F_m/C = 0.6$, i.e. 60 % of food requirements of consumers are satisfied by flux of C_{org} produced by migrating animals. But it should be emphasized once more that we are discussing here only the maximum possible transport of organic carbon by migrators.

Downward transport of organic matter with gut content of migrating animals

The possibility of such a transport is associated with the fact that, after feeding at the upper depth, the migrators may evacuate the gut content at the lower depth. Thus this unassimilated food is not eaten by other animals inhabiting the interval Δz, but it can be consumed below the depth z_l. In order that the organisms transport the unassimilated food downwards, the time required for its passage through their intestines, t_e must be more than the time t_m required to descend through the distance Δz. Therefore it is necessary to determine both intervals of time t_e and t_m. We shall do it for copepods.

The total evacuation of gut content by copepods accomplished by three defecations with the intervals between them equals t_{def} (Arashkevich 1975), i.e. gut passage time $t_e = 3t_{def}$. The quantity of unassimilated food C_{na} in relation to the food intake C is described as $C_{na} = (1 - U)\, C$. The intake in its turn is related to the production P as $C = P/UK_2$. Using the expression $P = w_0 W^{0.75}/T_0\, \tau$ for the production (Tseitlin 1981 a) we obtain:

$$C_{na} = (1 - U) w_0 W^{0.75}/24UK_2 T_0\, \tau \quad (25)$$

where C_{na} is in units mg h^{-1},

$\tau = \exp(0.081(20\text{-}t))$. t - temperature, °C.

Let us assume that the feeding of migrators occurs during the eight hours. Since unassimilated food is evacuated by copepods at the moments of defecations with the average frequency ν_{def} (h^{-1}), we can write:

$$\nu_{def} = 8C_{na}/w_{pel},$$

where w_{pel} is the weight of fecal pellet. Instead of the last expression one may use the interval of time between successive defecations:

$$t_{def} = 1/\nu_{def} = w_{pel}/8C_{na} . \quad (26)$$

In order to determine t_{def}, it is necessary to

find the average weight of fecal pellet w_{pel}. Volume of a pellet V_{pel} (mm^3) is related to the copepod body length l (mm) by the following equation (Petipa 1981):

$$V_{pel} = 0.000112\, l^3 . \quad (27)$$

If one designates as d_{pel} the density of a fecal pellet, then $w_{pel} = V_{pel}\, d_{pel}$. Using this expression and the relation between body weight and body length of copepod $W = 0.045\, l^3$ (Gruzov and Alekseeva 1970), we obtain:

$$w_{pel} = 0.0025\, d_{pel} W \quad (28)$$

where W is the weight of a copepod in milligrammes. The very similar result follows from the data of E.Arashkevich as well. Substituting equations (25) and (28) into the equation (26), we find:

$$t_{def} = 0.0075\, UK_2 T_0 d_{pel} W^{0.25} \tau/(1-U) \quad (29)$$

According to Bruland and Silver (1981), $d_{pel} = 1.2$ mg mm^{-3}. Using in equation (29) $T_0 = 33$ day, $U = 0.6$ and $K_2 = 0.25$, one receives:

$$t_e = 3 t_{def} = 0.33\, W^{0.25} \tau , \quad (30)$$

where t_e is the gut passage time in hours.

As it follows from equation (30), the gut passage time weakly depends on copepod weight W. At the same time, there is a great individual variability of t_e. For instance, it may differ more than by a factor of seven (Dagg et al. 1989) under the influence of factors, that put out of account by equation (29). The same change might arose with the increase of W by more than three thousand times. The experimental data (Arashkevich 1975, Arashkevich and Tseitlin 1978, Dagg et al. 1989, Timonin et al. 1992) show that the typical gut passage time is about 0.5 h. Calculation by means of equation (30) gives the values which are in good agreement with this result.

The typical range of diel vertical migrations Dz is more than 100 m (Table 1). The sinking velocities of copepods are at average 10 m h^{-1} and rarely exceed 20 m h^{-1}. Thus the descent time t_m is usually more than five hours, i.e. $t_m >> t_e$.

Hence unassimilated food cannot be transported by small animals such as copepods, which comprise most part of the mesoplankton, since their descent time is measured in hours while their digestion time usually does not exceed one hour. But in the case of macroplankton, with a considerably longer digestion time, this possibility is not excluded. Finally, we must take into account the time which the macroplankton spend at the upper depth. This time is sufficient for organisms to evacuate their gut content at least once, so that no more than a half of unassimilated food is carried downward.

Conclusions

We have considered two possible means of downward transport of organic matter with diel vertical migrations. The first is transport of live organic matter included in the tissues of migrator bodies, while the second is transport of organic matter in the form of gut content. In the first case the magnitude of the transport is given by the difference between the amount of migrators consumed by predators at the lower depth and the proportion of their own food intake at this depth. We evaluated the maximum possible transport as being up to 23% of the production of mesoplankton (300-500 m layer) and up to 11% of the production of macroplankton (700-900 m layer). However, we have shown that even if a small portion (a few percent) of diel food intake is consumed in deep waters, the transport of organic matter by these means is negligible. We should also note that our numerical estimates are based on data from only one region of ocean.

The transport of organic matter in the form of gut content of migrators is also very small (Tseitlin 1981 b). It actually takes place only in the case of macroplankton organisms. Diel migrations of organisms can increase the flux of organic matter into the deep layer, but in the tropical regions of the oceans this increase is apparently very small. It seems impossible to say anything further on the basis of existing data on feeding of migrating animals, but the little quantity of organic matter which can be transported in vertical migrations does not mean that its trophic role is unimportant: it may constitute a considerable proportion in the feeding of population at the next trophic level which does not migrate from the depth z_l.

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Происходит ли перенос органического вещества при суточных вертикальных миграциях животных в океане?

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РЕЗЮМЕ. Рассмотрены два возможных пути переноса органики вниз при суточных вертикальных миграциях: 1) перенос органики, заключенной в телах мигрантов, и 2) перенос с фекалиями мигрантов. Величина переноса в первом случае определена как разность между величинами потребления мигрантов хищниками на нижней глубине обитания и долей их собственного рациона, получаемой на этой глубине. Показано, что уже при очень малом питании внизу переноса органики таким путем либо не происходит, либо он очень мал. Максимальная величина потока $C_{орг}$, создаваемого мигрантами, не превышает 8% потока $C_{орг}$, образуемого погружающимся детритом. Во втором случае перенос возможен лишь с фекалиями макропланктонных животных и составляет очень малую долю от потока детрита сверху.